

A NEW EURYPTERID FROM THE LATE ORDOVICIAN TABLE MOUNTAIN GROUP, SOUTH AFRICA

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ABSTRACT. An exceptionally preserved eurypterid, *Onychopterella augusti* sp. nov., is described from the Soom Shale Member of the Cedarberg Formation, Table Mountain Group, of Cape Province, South Africa, extending the temporal range of this genus into the late Ordovician and providing the first occurrence in Gondwana. *O. augusti* can be distinguished from related taxa by the shorter proportions of the postabdomen, lanceolate telson, the large anterior projection of podomere seven and the long terminal spine of the sixth prosomal appendage. The level of preservation is such that traces of internal soft tissues, rarely preserved in eurypterids, can be discerned, including muscular tissue associated with the appendages and telson, respiratory structures (areas of branchial chambers), and an apparently spiral valve in the anterior part of the alimentary canal.

THE Table Mountain Group is a 3000 m thick, predominantly arenitic unit that is widely exposed in the mountains of south-western Cape Province, South Africa. A finer grained unit, the Cedarberg Formation, forms a conspicuous recessive marker horizon throughout the area of outcrop, and is divided into two members: the Soom Shale Member and the Disa Siltstone Member (Text-fig. 1). The Soom Shale is up to 15 m thick, and comprises thinly laminated fine siltstones that are black when fresh, but pale grey when weathered. This deposit is becoming well known for producing important and exceptionally preserved fossils, including conodonts (Theron *et al.* 1990; Aldridge and Theron 1993) and naraoid arthropods (Fortey and Theron 1995). In this paper we report the discovery of two specimens of a new eurypterid, *Onychopterella augusti* sp. nov., one of which has soft tissues preserved.

Both specimens were collected from a locality on the Keurbos farm, about 11.5 km south-east of Clanwilliam, north of Cape Town (Text-fig. 1), where the lower part of the Soom Shale is exposed overlying conformably the diamictites of the Pakhuis Formation. The eurypterids came from loose blocks freed during excavation of the exposure face, so their precise position in the section is unknown. Fossils currently known from Keurbos are not age-diagnostic, but the Soom Shale Member in the Hex River Mountains, some 100 km away, has yielded the trilobite *Mucronaspis olini*, indicative of a late Ashgill age (Cocks and Fortey 1986).

Eurypterids are rare fossils in South Africa. Waterston *et al.* (1985) described the large *Cyrtoctenus wittebergensis* from the Carboniferous Witteberg Group of Cape Province, and two other specimens from Witteberg sediments near Grahamstown, described by Seward (1909), were referred to *Hastimima sewardi* (Strand, 1928) and later, with reservation, to *Hibbertopterus* (Kjellesvig-Waering 1966). Arthropod tracks from the early Ordovician Graafwater Formation, Table Mountain Group, described by Taljaard (1958), Rust (1967) and Anderson (1975) may in some instances be attributable to eurypterid activity (A. Seilacher, pers. comm.). Elsewhere in Africa, eurypterids have been recorded only from farther north; pterygotid fragments were noted from sediments of early Silurian age near Denate in the Atlas mountains of Morocco by Waterlot and Leveque (1960), and carcinosomatid and pterygotid remains were reported from the Acacus Formation (mid Silurian) of Tadrart in Libya (Depitout 1962). Borehole samples from Lower Devonian strata in the Sahara have yielded indeterminate cuticular remains and areas of gill tract

(Taugourdeau 1967, 1978). Depitout (1962) reported abundant eurypterid remains from the upper Silurian of Algeria which he referred to indeterminable pterygotids and *Eurypterus*, although Caster and Kjellesvig-Waering (1964) later suggested that many might be carcinosomatids. A possible pterygotid tergite from northern Libya was recovered from well drilling in the Silurian Tanezruft shale (Kjellesvig-Waering 1964).

Elsewhere in Gondwana, a few eurypterids of Lower Palaeozoic age have been reported from South America. A number of indeterminate tergites and a telson with a serrate lateral margin were described from the Llanvirn of Bolivia by Toro and Pérez (1978). Indeterminate eurypterid remains were also noted from the Yerba Loca Formation (middle Ordovician) of Jachal, Argentina (Ramos and Blasco 1975). *Slimonia boliviana* was described from the Kirusillas Formation (upper Silurian) of Pojo, Bolivia (Kjellesvig-Waering 1973). In the Upper Palaeozoic of Brazil, *Hastinima* has been reported from the Permian of Santa Catarina (see Waterston *et al.* 1985 for review) and Sao Paulo states (Mezzalana 1951), and from the Lower Devonian Picos Formation of Piaui State (Caster 1947). Kjellesvig-Waering (1960), however, concluded that the latter two occurrences were not determinable. Indeterminate remains were noted from the Gamoneda Formation (Lower Devonian) of Tarija, Bolivia (Eldredge and Branisa 1980). *Pterygotus bolivianus*, from the Middle Devonian of La Paz, Bolivia is the only record of a pterygotid from South America (Kjellesvig-Waering 1964). Additionally, a possible adelopthalmid was recorded from the Middle Devonian Punta Negra Formation of San Juan, Argentina (Kjellesvig-Waering 1960).

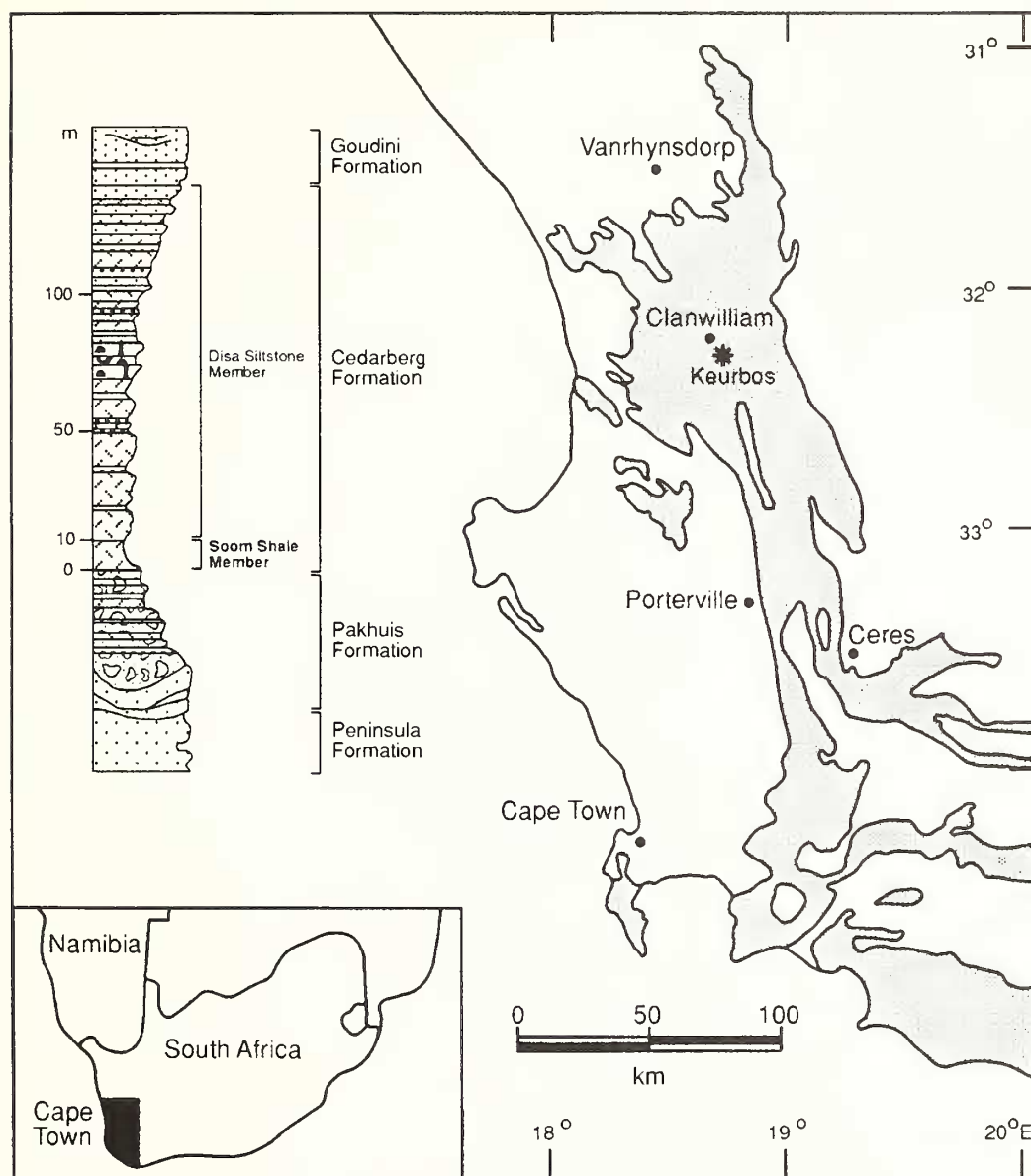
Eurypterid records from Australia, reviewed by Selden (1993), include cuticle fragments from South Yarra, Melbourne, referred to *Pterygotus australis* (M'Coy 1899). Fragmentary specimens, collected at Cootamundra, New South Wales, were referred originally to *Hughmilleria* (Gill 1951), but Caster and Kjellesvig-Waering (1953) later concluded that they were indeterminable, with the largest belonging probably to a pterygotid. An unusual carapace with large eyes and a frilled posterior margin, described as *Melbournopterus crossotus*, was found in upper Silurian siltstones near Heathcote, Victoria (Caster and Kjellesvig-Waering 1953) in association with monograptids. A specimen from the Devonian Gogo Formation, Western Australia was referred tentatively to *Rhenopterus* by Waterston (*in* Rolfe 1966), but awaits formal description. Eurypterid fragments have also been reported from Lower Devonian siltstones at Kinglake West, Victoria (Jell 1992).

Eurypterids previously recorded from the Lower Palaeozoic of Gondwana are all referable to the Carcinomatidae and Pterygotidae (Plotnick 1983), recognized as representatives of the most marine ecological phase of eurypterids (Kjellesvig-Waering 1961). Until now, *Onychopterella* was known only from the Silurian of North America. The occurrence in the Soom Shale extends its temporal range into the late Ordovician, and provides the first record of the Erieopteridae from Gondwana.

MATERIAL AND TERMINOLOGY

The holotype (GSSA C373a, b) comprises the part and counterpart of a complete eurypterid (Pl. 1; Pl. 2, figs 1–3; Text-figs 2–3). The fragile counterpart is broken into two pieces, one of which has been preserved with a clear consolidant to prevent further degradation. The paratype (GSSA C427a, b) consists of part and counterpart, each a single piece, displaying only the incomplete opisthosoma and the distal podomeres of appendage VI on the edge of the block (Pl. 3, figs 1–4; Text-fig. 4). After initial splitting to separate part and counterpart on each specimen, no further preparation was undertaken. The specimens are deposited in the collections of the Geological Survey of South Africa, Silverton, Pretoria (GSSA).

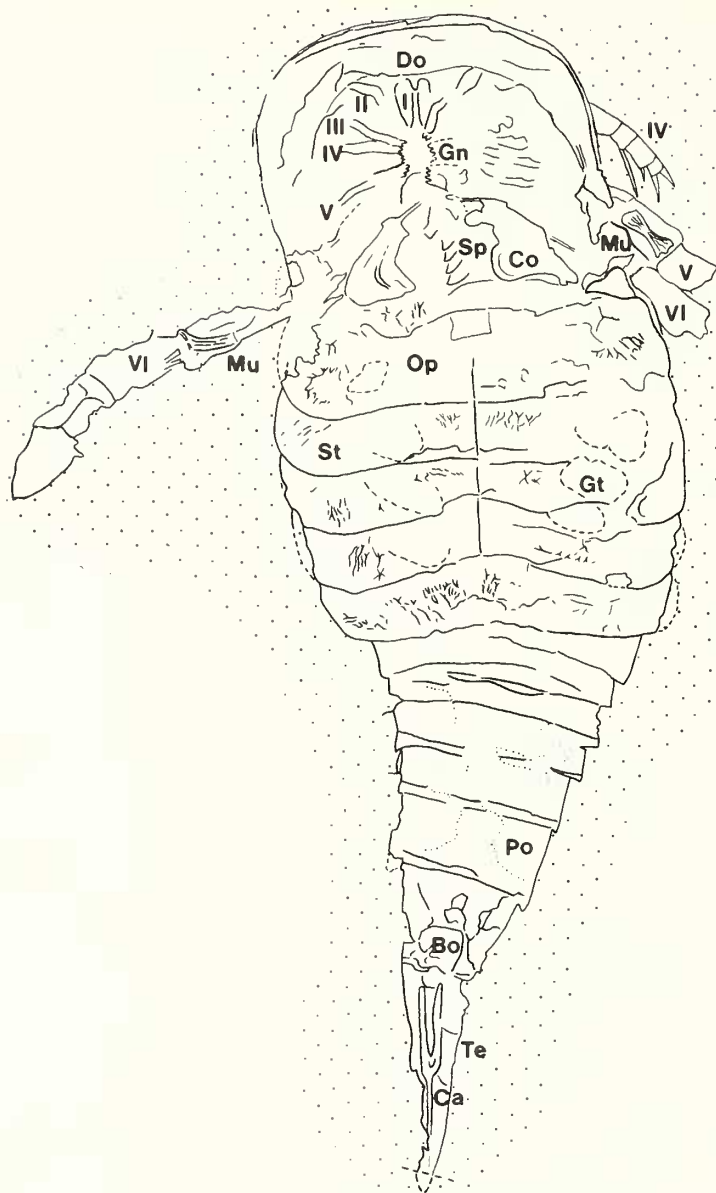
The specimens are described using empirical standards of terminology, following Tollerton (1989) to ensure less subjectivity. 'Prosoma' is used in preference to 'cephalothorax' to describe the anterior tagma, and 'carapace' is used for the dorsal shield of the prosoma. 'Preabdomen' and 'postabdomen' are employed in preference to 'mesosoma' and 'metasoma' respectively, to describe the anterior and posterior units of the abdomen. Prosomal appendages are denoted by Roman numerals, with individual podomeres numbered from proximal to distal.



TEXT-FIG. 1. Map of the south-western region of Cape Province, showing the outcrop of the Table Mountain Group (shaded) and the fossil locality at Keurbos (asterisk). The stratigraphical section shows part of the Table Mountain Group, including the Soom Shale Member.

PRESERVATION

The holotype part (GSSA C373a) occurs on a 20 mm thick layer of finely laminated siltstone and consists of an external mould of the ventral surface exhibiting internal features of the prosoma and telson (Text-fig. 2). The taphonomy of fossils in the Soom Shale is currently under investigation, but it seems likely that the soft tissues of the eurypterid have been preserved by early phosphatization.



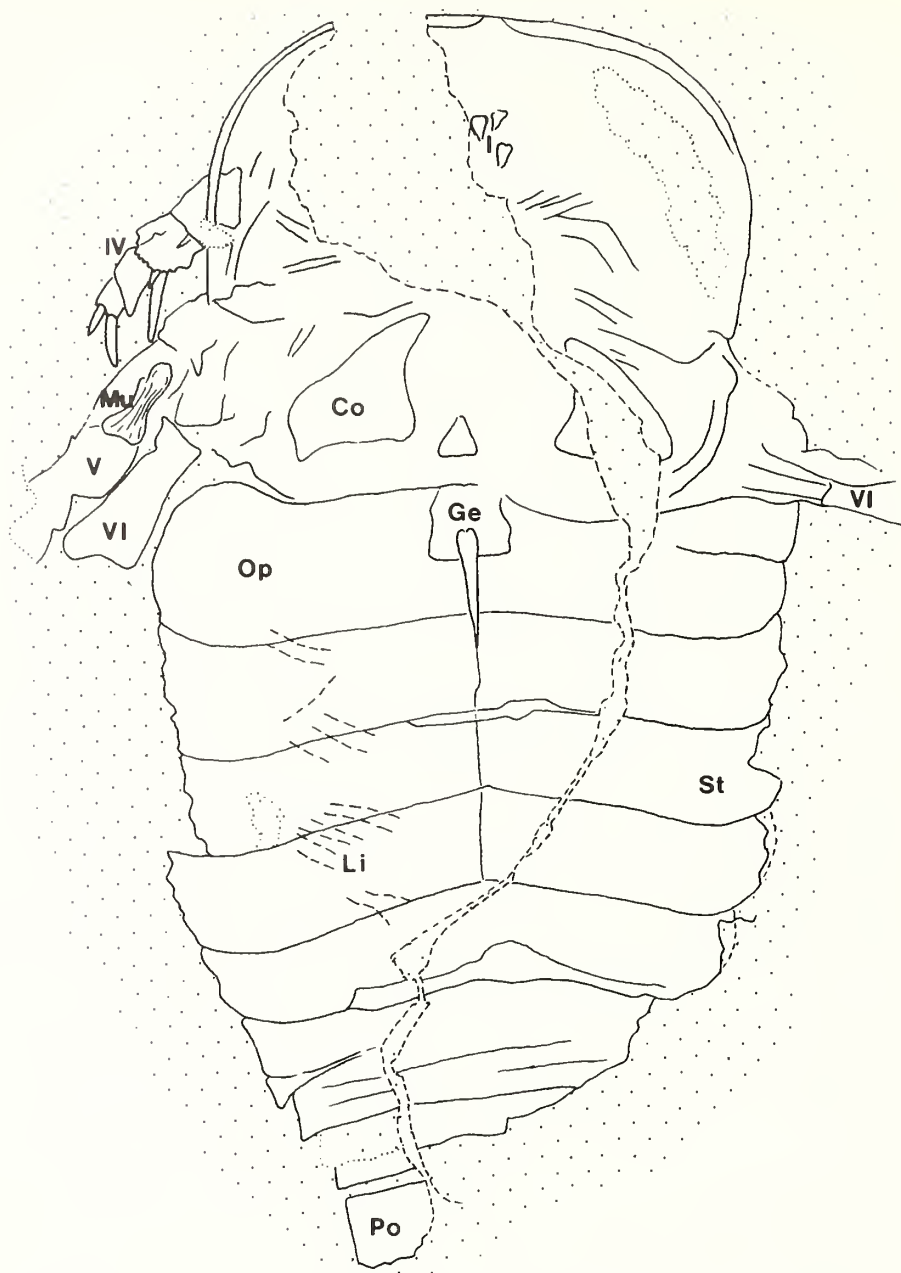
TEXT-FIG. 2. *Onychopterella augusti* sp. nov. Camera lucida drawing of the holotype, GSSA C373a. Prosomal appendages denoted by Roman numerals. Bo, boss-like structure of pretelson and proximal part of telson; Ca, medial carina; Co, coxal muscles of appendage VI; Do, doublure; Gn, gnathobases of prosomal appendages; Gt, gill tract or infilled branchial chambers; Mu, muscular tissue associated with appendages; Op, genital operculae; Po, postabdominal segment; Sp, spiral valve of alimentary canal; St, preabdominal sternite; Te, telson; $\times 2.5$.

EXPLANATION OF PLATE I

Onychopterella augusti sp. nov.; GSSA C373a, holotype; Soom Shale Member, Cedarberg Formation, Table Mountain Group; Clanwilliam, Cape Province, South Africa; $\times 2.5$.



BRADDY *et al.*, *Onychopterella*



TEXT-FIG. 3. *Onychopterella augusti* sp. nov. Camera lucida drawing of the holotype, counterpart GSSA C373b. Prosomal appendages denoted by Roman numerals. Co, coxal muscles of appendage VI; Ge, trace of proximal part of genital appendage; Li, lineations on infilled branchial chambers; Mu, muscular tissue associated with appendages; Op, genital operculae; Po, small corner of postabdominal segment; St, preabdominal sternite; $\times 3.5$.

The majority of eurypterid fossils are exuviae (Clarke and Ruedemann 1912; Stormer 1934) and do not represent dead animals. The very rare preservation of gut structures in some eurypterids has been cited as evidence that these specimens were the remains of dead animals (Kjellesvig-Waering 1958b). However, the presence of gut structures cannot be used as the sole criterion to distinguish a moult from a dead animal, because in many arthropods parts of the gut are moulted during ecdysis. Moulded exoskeletons may be found complete, but are frequently preserved as disarticulated remains, dispersed by currents into individual podomeres and tergites. Internal tendonal tissues may be preserved in exuviae, as these are ectodermal in origin (Selden 1981). The preservation of the internal muscular tissues in the holotype indicates that this is the carcass of a complete dead animal. Soft tissues are not recognizable on the incomplete paratype, so we cannot determine whether it is a dead animal or an exuvia.

MORPHOLOGICAL RECONSTRUCTION

A reconstruction of the dorsal and ventral aspects of *Onychopterella augusti* is provided (Text-fig. 5). The majority of morphological features are preserved on the holotype, enabling an accurate reconstruction of most of the organism, based on this specimen. The shape of the lateral eyes is inferred by comparison with *O. kokomoensis* (Miller and Gurley, 1896) to be reniform (concave outer margin with flatter inner margin); they are approximately one-quarter the length of the carapace and situated in a centrimesial position (see Tollerton 1989). The ocelli are reconstructed as situated slightly posterior to the position of the lateral eyes, near the mid-line of the prosoma, as in *O. kokomoensis* (Clarke and Ruedemann 1912, pl. 25, fig. 2). Despite these authors' statement that the ocelli were not apparent, the artist had noted their position.

Where possible, the anterior appendages (I–V) were reconstructed according to available material, with any unknown parts inferred from *O. kokomoensis*. The reconstruction of appendage VI is based on the paratype (GSSA C427a); the coxae, not present on this specimen, were inferred from the shape of the muscle masses, and from comparisons with the subrhomboidal coxae of *O. kokomoensis*.

The metastoma, not preserved on either specimen, is reconstructed according to that of *O. kokomoensis* as small, approximately one-third the length of the carapace and oval in form, the anterior margin slightly convex and emarginate, a little narrower than the posterior margin.

Only a trace of the proximal part of a genital appendage is preserved on the counterpart of the holotype, and is reconstructed by inference from a specimen of *O. kokomoensis* (Clarke and Ruedemann 1912, pl. 26, fig. 2) as a type A appendage, with paired basal plates, reaching the posterior margin of the third sternite and ending in a tricate termination (Tollerton 1989).

The ventral surface of the opisthosoma can be reconstructed accurately from the holotype but the segmentation of the dorsal surface is inferred from *O. kokomoensis*. The shape of the telson can be determined accurately, although its external morphology is reconstructed according to *O. kokomoensis*, with a single medial carination on the dorsal surface.

The paratype was approximately 143 mm long, by comparison of its proportions with the holotype, although the postabdominal segments of the former are proportionally slightly shorter than those of the latter. This variation is considered solely ontogenetic, the larger individuals having slightly shorter postabdomens.

RELATIONSHIPS

Two species of *Onychopterella* have been recorded previously, both from North America. They have distinct dolichopteroid or stylonuroid characteristics in that they have slender walking legs and narrow swimming legs, a feature which may be of phylogenetic importance (Kjellesvig-Waering 1958a). In this respect, *Onychopterella* is intermediate in form between the Eurypteroidea and the Stylonuroida.

O. kokomoensis is the commonest species in the late Silurian Kokomo eurypterid fauna, Indiana, yet specimens are rare in museum collections. A brief description is given for comparison with *O. augusti*. The body is small and relatively broad, about three and a half times as long as it is wide. The subquadrate carapace, slightly wider than long, has rounded anterior angles and a broad doublure. The lateral eyes are reniform, of medium size, and lie on the anterior half of the prosoma. Appendages III–VI are known, VI being slender and bearing a long terminal spine, more than half as long as podomere 8 and slightly curved. The coxae of appendage VI are relatively small and subrhomboidal in general outline. The oval metastoma is small, measuring little more than one-third the length of the carapace. The genital appendage is seen clearly only in one specimen, reaching the posterior margin of the third sternite with paired basal deltoid plates visible in faint outline. The abdomen is a little wider than the prosoma, the preabdomen as wide as long, the postabdomen relatively short and compact, longer by one-third than the preabdomen. The postabdominal segments increase gradually in length posteriorly, the last being twice as long as the first, but only one-third as wide. The last postabdominal segment is produced into two short broad lobes with blunt extremities. The telson is short and thick (clavate), a little more than one-fifth the length of the body. Ornamentation of the last postabdominal segment consists of small, evenly distributed, sharply angular or pointed scales (Clarke and Ruedemann 1912).

Onychopterella pumilis was described from a single, nearly complete, well preserved specimen, displaying the original coloration of the integument, from the lower part of the early Silurian Essex (Edgewood) Limestone in Kankakee County, Illinois (Savage 1916). Only 39 mm long, it differs from *O. kokomoensis* in having proportionally slimmer prosomal appendages, a tapering preabdomen, and a pretelson segment which lacks epimeral prolongations. The telson is spike-like (rapidly contracting) rather than having a slight broadening at the posterior half (clavate) and the lateral eyes are more forwardly placed than in *O. kokomoensis*. The very small size and eye position suggest that this may be a juvenile (Kjellesvig-Waering 1958a), and the differences from *O. kokomoensis* may be solely ontogenetic.

FUNCTIONAL MORPHOLOGY

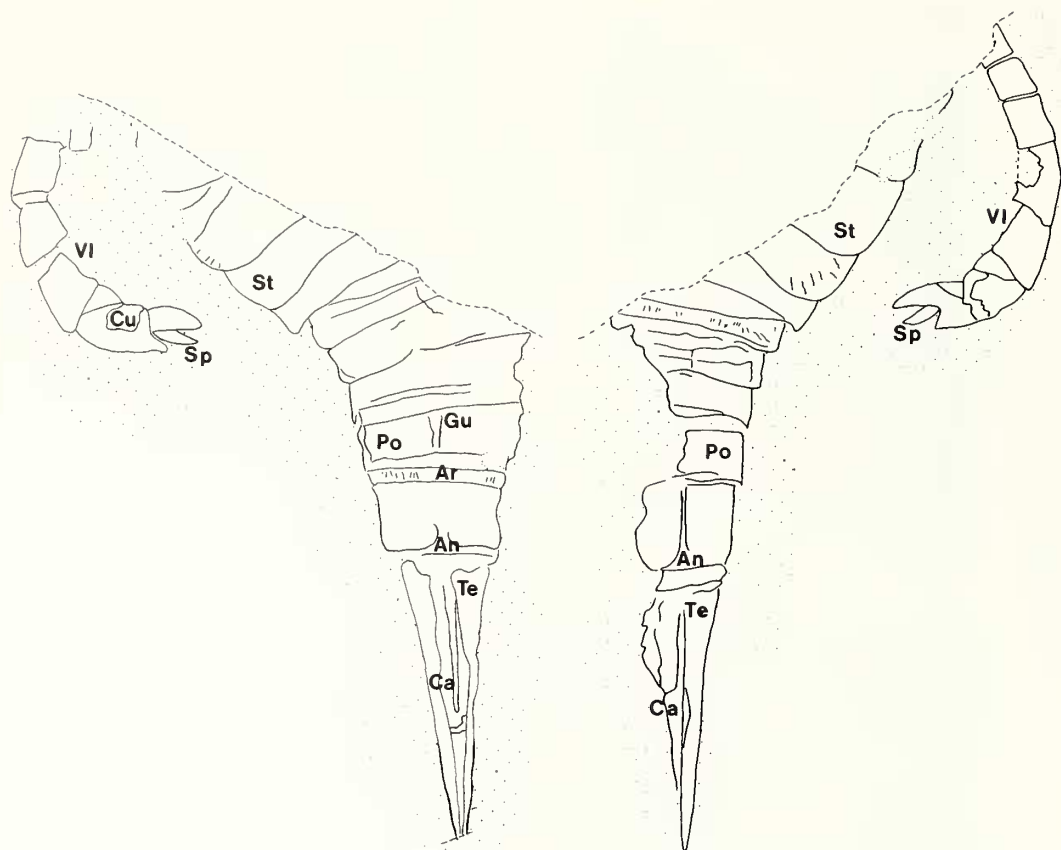
The level of preservation in these specimens is sufficient for the structure of many of the internal features to be discerned, providing information on the functional morphology. The spiral-shaped structure between the two coxal muscle masses of the prosoma probably represents an anterior portion of the gut. The arthropod gut is composed of three parts: the ectodermal stomodeum, comprising the oesophagus and the gizzard; the endodermal mesenteron, formed by the stomach and intestine; and the ectodermal proctodeum, formed by the rectum. In *Limulus*, a related extant chelicerate, food items, after mastication by the gnathobases, are passed down the oesophagus into a grinding chamber, the gizzard. Indigestible particles are regurgitated through the oesophagus, whereas food particles are passed posteriorly through a valve into the stomach. Two pairs of lateral diverticula, forming glandular caeca, secrete digestive enzymes into the stomach through two pairs of ducts. The intestine extends posteriorly into the opisthosoma and waste is egested through a short sclerotized rectum and out through the anus, located on the ventral side of the abdomen, just in front of the telson (Barnes 1980).

Alimentary canals have previously been described in *Carcinosoma newlini* (Ruedemann 1921; Kjellesvig-Waering 1958b), *Pterygotus (Acutiramus) macrophalmus cummingsi* (Clarke and

EXPLANATION OF PLATE 2

Figs 1–3. *Onychopterella augusti* sp. nov.; GSSA C373, holotype. 1, detail of prosoma; $\times 3.7$. 2, coxal muscles of appendage VI with a medial spiral alimentary structure; $\times 5.5$. 3, detail of appendage VI: internal musculature and proximal articulation of podomere V; $\times 5.2$.





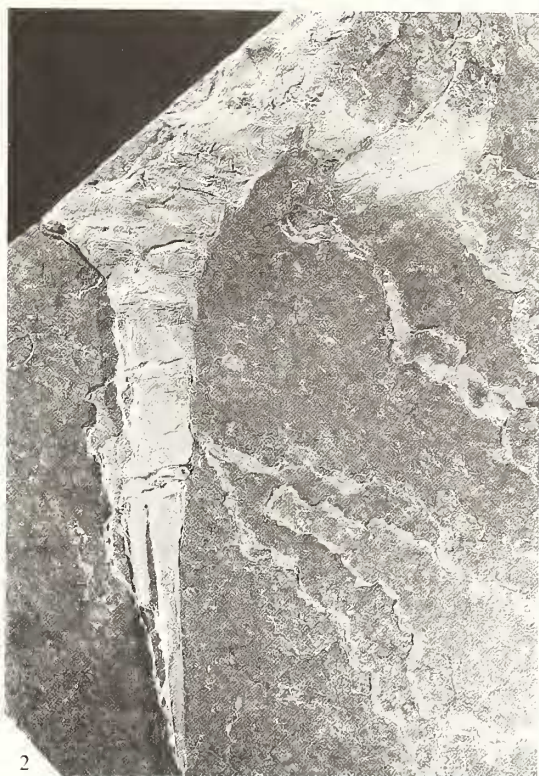
TEXT-FIG. 4. *Onychopterella augusti* sp. nov. Camera lucida drawings of GSSA C427a (right) and GSSA C427b (left). Prosomal appendages denoted by Roman numerals. An, anal opening of pretelson; Ar, arthrodial membrane; Ca, internal mould of medical carina; Cu, patches of cuticle; Gu, posterior portion of gut; Po, postabdominal segment; Sp, distal spine of podomere 8; St, preabdominal sternite; Te, telson; $\times 1.25$

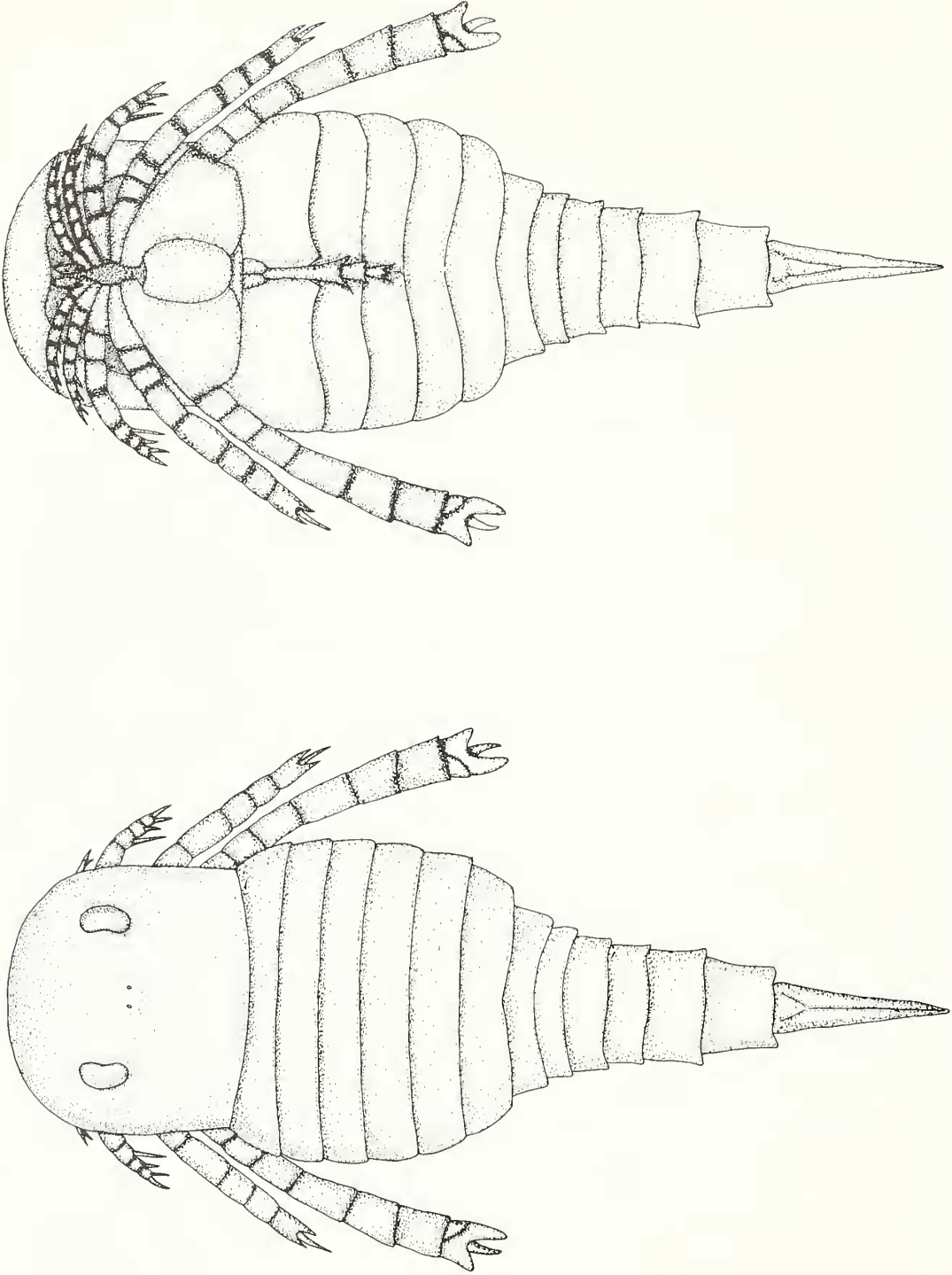
Ruedemann 1912) and *Eurypterus lacustris* (Heubusch 1962), where a depressed tubular structure with several transverse ridges, indicating a spiral morphology, is exposed along the mid-line of the pretelson.

A spiral valve, 80 mm long and consisting of five dextral whorls, was reported in *Cyrtotenus wittebergensis* (Waterston *et al.* 1985) near the posterior of the prosoma, but no equivalent structure has been described in any other eurypterid. Spiral valves developed independently in various fish groups as an adaptive response to the need to increase the absorptive area of the gut (Williams

EXPLANATION OF PLATE 3

Figs 1–4. *Onychopterella augusti* sp. nov.; GSSA C427, paratype. 1, part; $\times 1.1$. 2, counterpart; $\times 1.1$. 3–4, detail of distal podomeres of appendage VI; $\times 2.9$.





TEXT-FIG. 5. *Onychopterella angustii* sp. nov. Dorsal (left) and ventral (right) reconstruction; $\times 2$.

1972), although the enterospire occurs towards the posterior end of the digestive tract. It seems reasonable to suggest that similar structures could have evolved in some eurypterid groups for a similar function, although 'the presence of a spiral valve would depend upon the requirements of digestion and absorption which in turn may depend upon such factors as feeding habits and size which vary greatly from one type of eurypterid to another' (Waterston *et al.* 1985, p. 349). The sweep-feeding appendages of *C. wittebergeus* suggest that it was a sediment feeder, and the spiral structure apparently evolved to increase the absorptive area of the gut and to extract food from the sediment. The spiral structure observed in *O. augusti* may have had a similar function, acting as a valve to the mesenteron and increasing the absorptive area of this portion of the gut.

The internal morphology of prosomal appendage VI reveals something of the locomotory capabilities of this animal. The coxal muscles of appendage VI are elongate in an anterolateral orientation, suggesting that these relatively slender legs were maintained in a posterolateral orientation for walking in order to enable sufficient stability around the animal's centre of gravity. In eurypterids the coxae are usually directed transversely, except for the two posterior coxae which have a more posterolateral orientation (Hanken and Stormer 1975). The presence of elongate proximal podomeres and the terminal spine on the sixth prosomal appendage of onychopterellan eurypterids indicates their primitive condition as natatory organs and their functional adaptation to walking (Clarke and Ruedemann 1912).

The prominent boss-like structure at the proximal end of the telson is interpreted as a large area of muscles and tendons used for the articulation of the telson. It appears similar, in many respects, to the enigmatic *Marsupipterus sculpturatus*, known only from its telson, from the Silurian of the Welsh Borderlands (Caster and Kjellesvig-Waering 1955). Originally considered a stylonurid eurypterid, it was interpreted by Rolfe (1963) as a phyllocarid crustacean of uncertain affinity, and was therefore rejected from the Eurypterida by Caster and Kjellesvig-Waering (1964). This species, whatever its affinity, has a large elliptical pouch on the ventral side of the telson, which was attributed a cloacal (storage prior to excretion) function by Caster and Kjellesvig-Waering (1955). However, it is probable that the anus of most eurypterids opened through thin cuticle between the telson and the pretelson, as in *Limulus* (Selden 1984). It is more likely that the elliptical opening of *M. sculpturatus* reflects the presence of a large muscular or tendonal mass similar to that of *O. augusti*, capable of moving the telson to defend the dorsal surface of the eurypterid and enabling overturning while on the substrate. Examination of *M. sculpturatus* from the British Geological Survey collections shows that the cuticle of the ventral surface may have broken away to reveal the opening, which is an internal feature of the telson. The apparent differences in this structure between *O. augusti* and *M. sculpturatus* are regarded as preservational: only the cuticle is preserved in *M. sculpturatus*, revealing a hollow depression, whereas in *O. augusti* the muscular tissues are preserved as an upstanding boss-like structure.

PALAEOECOLOGY

Eurypterids are comparatively scarce as fossils, as they typically inhabited marginal marine, deltaic and estuarine environments. *Onychopterella* was thought by Kjellesvig-Waering (1958a) to inhabit brackish and possibly marine water. The mode of life of these eurypterids was undoubtedly nekto-benthic; they were capable of swimming but probably lived mostly on the substrate. Clarke and Ruedemann (1912, p. 216) concluded that: 'It was not so well adapted to a swimming lifestyle as forms such as *Eurypterus remipes* as is shown by the relatively small coxae, the less developed and more slender swimming legs, the presence of a terminal spine, obviously used in walking, and the shorter and stouter postabdomen. The extremely broad doublure may indicate an adaptation of the front edge to shovelling or digging.'

The Cedarberg Formation was deposited during a glacioeustatic rise in sea level and probably represents the outwash silt and mud from the retreating ice sheets, deposited in a glaciolacustrine to shallow marine environment (Theron *et al.* 1990). The very fine laminations of the Soom Shale

show no penetrative bioturbation, indicating that conditions were anoxic below the surface. *Onychopterella augusti* is found in association with *Orbiculoidea* and infrequent lingulid brachiopods, orthoconic nautiloids, naraoiid trilobites (Fortey and Theron 1995), conodonts (Theron *et al.* 1990), and various enigmatic organisms. The eurypterid would have been a top predator in this ecosystem, probably feeding on other arthropods, worms and perhaps conodonts.

SYSTEMATIC PALAEONTOLOGY

Order EURYPTERIDA Burmeister, 1843

Suborder EURYPTERINA Burmeister, 1843

Superfamily EURYPTEROIDEA Burmeister, 1843

Family ERIOPTERIDAE Tollerton, 1989

Diagnosis. Legs II–IV spiniferous, *Eriopterus* type; leg V nonspiniferous, *Eurypterus* type; leg VI swimming leg, *Eriopterus* type (Tollerton 1989).

Genus ONYCHOPTERELLA Stormer, 1951

Diagnosis. Prosoma subquadrate; walking legs undifferentiated, long narrow, without spines except at distal end; swimming legs inconspicuous, very narrow; pretarsus very long, spike-like; no contraction of opisthosoma; metastoma rounded posteriorly and sub-cordate anteriorly; genital appendage not well known; ornamentation comprises small pointed scales (Miller and Gurley 1896).

Remarks. The shape of the telson of *Onychopterella* was described as clavate by Tollerton (1989), but that of *O. pumilis* is styliform and that of *O. augusti* lanceolate. Therefore telson morphology is here considered a specific, rather than a generic character.

Onychopterella augusti sp. nov.

Plates 1–3; Text figures 2–5

Derivation of name. After August Patrick Pedro, who found the holotype during a collecting trip led by JNT and RJA in 1991.

Material. Holotype, GSSA C373a, b: part and counterpart (in two parts); complete prosoma (anterior appendages II–IV complete, V and VI partial), opisthosoma and telson. Paratype, GSSA C427a, b: part and counterpart; incomplete opisthosoma, telson and distal podomeres of appendage VI.

Horizon and locality. Late Ashgill, Soom Shale Member of Cedarberg Formation, Table Mountain Group. Keurbos farm, near Clanwilliam, North of Cape Town, South Africa, longitude 18° 58' E, latitude 32° 18' S.

Diagnosis. Subquadrate prosoma, broad doublure (approximately one-fifth the length of the carapace), short postabdomen and short lanceolate telson; pretelson lacks epimeral prolongations; appendage VI has podomere 8 drawn into two distal projections, the anterior projection much larger than the posterior, both emarginate with long terminal spine, projecting to the length of the anterior projection of podomere 8.

Description. Specimen GSSA C373 (holotype). The body is small (Pl. 1; Text-fig. 2) with a total length of 73.8 mm, approximately three times as long as wide with a first order differentiation of the opisthosoma (Tollerton 1989). The subquadrate prosoma, length 18.7 mm, width at base 21.0 mm, expands slightly anteriorly with a lateral angle of 86°, giving the prosoma something of a horse-shoe shape. The internal structure of the

prosoma can be discerned by colour variations in the internal matrix; the anterior prosomal appendages (I–III), coxal muscles and anterior doublure are preserved in grey against a pale yellow matrix (Pl. 2, fig. 1). There are no details of the eyes or median dorsal ocelli because these are external features. The broad doublure of *Erieopterus* type (Tollerton 1989), clearly evident towards the lateral margins of the carapace, can be followed around the anterior margin where it is slightly concave in the medial region, approximately one-fifth the total length of the prosoma.

Within the medial region of the prosoma, a trace of the coxal gnathobases of appendage VI can be distinguished, those of the right set of appendages more evident than the left. It is not possible to distinguish which teeth belong to which coxa, although the posterior coxal gnathobase appears to bear several teeth. Faint impressions of the anterior appendages project radially away from the oral region; individual podomeres of these appendages are indistinguishable.

The anterior three appendages of the prosoma are poorly preserved, not projecting beyond the lateral margins of the carapace. The chelicerae (appendage I) are preserved as hollow depressions and no details of individual podomeres can be seen. Appendage II is seen best on the left side of the prosoma, projecting forward from the medial region, turning left and following the marginal rim of the carapace, ending in a faint bifid impression. Appendage II on the right side of the prosoma is less clearly preserved as is Appendage III on both sides of the prosoma because it does not project beyond the margin of the carapace and is discernible only as colour variations in the internal matrix.

Appendage IV is best observed on the right side of the carapace, well preserved as a dark grey impression beyond the lateral margin of the carapace. The distal podomeres (4–8) are evident, enabling description, but the more proximal podomeres, within the outline of the carapace, are indistinct. The distal part of podomere 4, preserved length 2.1 mm, width 2.0 mm, shows no evidence of spinosity. Podomere 5, length 2.1 mm, width 2.3 mm, is square, although its distal margin is less clearly preserved; a long spine 2.9 mm long, projecting posteriorly from its distal margin, is covered in small black striae. Podomere 6, length 2.0 mm, width 1.3 mm, has a more rectangular outline. A small spine, length 0.7 mm, projects from its distal margin. Podomere 7, 1.3 mm long and 1.1 mm wide, small and subquadrate in general outline, has a small distal spine, length 1.3 mm. Podomere 8 is short, length 2.0 mm, and spinose, showing traces of small striae.

Appendage V is well preserved beyond the right lateral margin of the carapace, with evidence of the internal musculature, but many of the distal podomeres are missing. Podomere 4, preserved length 2.5 mm, width 2.3 mm, is preserved distally yet is indistinct within the confines of the carapace. Podomere 5, rectangular in outline, 4.5 mm long and 2.1 mm wide, is preserved entirely, displaying evidence of the internal musculature, constricted medially such that approximately one-third of the width of the podomere appears to have been muscular tissue. At the proximal and distal margins of this podomere the muscle tissue expands to the full width of the podomere. Several parallel striations may represent the original muscle fibres. Podomere 6, preserved length 5.9 mm, width 2.2 mm, has a rectangular outline with no evidence of any spinosity. It is partially preserved, its distal part incomplete at the edge of the specimen.

Appendage VI is poorly preserved on the right side of the carapace; only podomere 4 is fully preserved with a trace of the distal margin of podomere 3. No evidence of the proximal podomeres is seen within the carapace, but there are two broadly triangular structures, preserved in a dark grey matrix near the posterior of the prosoma (Pl. 2, fig. 2). The position and size of these structures indicate that they are the large coxal muscles of this appendage. The shape of these coxal muscle masses, as broad as they are long, suggests that these coxae were subrhomboidal in outline. Appendage VI is best preserved on the left side of the carapace (Pl. 2, fig. 3). Podomere 4, preserved length 7.0 mm, width 2.6 mm, projects beyond the carapace, with evidence of the internal musculature constricted medially and expanding distally to the full width of the podomere. Striations inside the podomere may represent original muscle fibres. A convex structure at the distal end of this podomere probably represents a large mass of muscular tissue. The proximal margin of podomere 5 has a notch-like structure, perhaps representing a site of strong articulation with the preceding podomere. An impression of this internal musculature continues into podomere 5, medially constricted and expanding towards the proximal and distal margins. The anterior margin of podomere 5 is broken away and the posterior margin obscured by sediment such that only 5.7 mm of its length and 2.6 mm of its width can be discerned. Of podomere 6, 3.6 mm of its length and 2.6 mm of its width is preserved. Evidence of the internal musculature continuing down the appendage is seen as a medial colour variation. Podomere 7 begins to broaden, reflecting a widening of the appendage into the distal paddle. The posterior and distal margins of podomere 7 are covered by sediment; only 5.2 mm of its length and 5.2 mm of its width are preserved with no evidence of podomere 8 or the terminal spine.

No evidence of the metastoma (post-oral ventral plate) can be seen, but a tubular structure, length 3.1 mm, is identifiable between the two coxal muscle masses of appendage VI (Pl. 2, fig. 2). Four constrictions with

diagonal lineations suggest that this is a sinistral spiral structure and probably represents an anterior portion of the alimentary canal. There is no evidence of a genital appendage.

The opisthosoma is slightly wider than the carapace, expanding to its greatest width in the middle of sternite 2. The preabdomen, a little wider than long, is fully preserved except for the lateral margins of sternites 4 and 5. The genital operculae (sternite 1), length 5.7 mm, width 24.4 mm, are a little larger than the posterior sternites although their anterolateral margins are indistinct. The sternites are several times wider than long, their posterior margins moderately concave in their medial region, their lateral margins broadly rounded. The lengths and widths (at their widest part) of the preabdominal sternites are: sternite 2, length 3.4 mm, width 24.9 mm; sternite 3, length 3.4 mm, width 24.4 mm; sternite 4, length 3.4 mm, width 22.8 mm; sternite 5, length 4.1 mm, width 20.2 mm; sternite 6, length 2.6 mm, width 16.6 mm. The first four sternites have raised areas representing infilled branchial chambers or areas of soft gill tract respiratory tissue (Pl. 1; Text-fig. 2). These ovoid structures, those of the genital operculae being a little smaller than the others, occur on both sides of the body and have parallel, diagonal lineations on them, perhaps representing the internal structure of the lamellate gills (see Manning and Dunlop 1995). Dendritic structures occur over the entire abdomen but are more numerous towards the posterior of sternite 5. These structures most probably represent crenulations in the cuticle due to preservation and do not represent any original internal feature.

The preabdomen is relatively broad until the short postabdomen, where the segments contract gradually to the tapering telson. The postabdominal segments gradually increase their length posteriorly, the last being approximately twice as long as the first, although only half as wide. The dimensions of the postabdominal segments are: segment 1, length 2.6 mm, width 13.2 mm; segment 2, length 3.4 mm, width 11.7 mm; segment 3, length 3.0 mm, width 10.4 mm; segment 4, length 4.1 mm, width 9.3 mm; segment 5 (pretelson), length 5.7 mm, width 7.3 mm. The first few segments of the postabdomen are partially telescoped into one another and the segmentation is somewhat confused. The posterior three segments have areas of sediment pervading their medial region. The posterior lateral margin of each postabdominal segment is produced into small epimera. The distal end of the pretelson has a large boss-like structure upstanding from the specimen and extending into the proximal part of the telson. This structure probably represents an area of muscular or tendonal tissue attachment. Posterior to this, two small ridges converge about half-way along the telson and continue as a single ridge to the end. The left hand side of the telson is partly obscured by sediment and the terminal point is missing. The telson, length 13.7 mm, width at base 4.1 mm, approximately one-fifth the length of the body, gradually tapers into a lanceolate shape (Tollerton 1989).

The prosoma of the counterpart, GSSA C373b (Text-fig. 3), has a large medial fracture but the lateral margins of the carapace are evident. The anterior appendages (I–III) are obscured by the internal matrix but the more posterior appendages are apparent. No evidence of the gnathobases are preserved on this specimen as a result of the fracture.

Appendage IV is well preserved on the left side of the carapace. Podomeres 4–8 are preserved beyond the lateral margin but the more proximal podomeres, within the carapace, are indistinct. Podomere 5 shows the long spine projecting from the distal end. Podomeres 6 and 7 have shorter distal spines. Podomere 8 is short and spinose.

Appendage V is represented by podomeres 4–6, well preserved on the left hand side of the carapace; the distal podomeres are missing. Podomere 4 is distally preserved yet indistinct within the carapace. Podomere 5 shows the internal musculature.

Appendage VI is poorly represented on the counterpart. Podomere 4 projects beyond the carapace on the left side; on the right side only podomere 4 and a small corner of podomere 5 can be seen. The coxal muscles are evident towards the posterior of the prosoma, the left one preserved as a shallow depression; the right depression is less clearly evident due to the fracture in the carapace.

The metastoma is not preserved on this specimen. There is a small triangular structure, representing one whorl of the spiral alimentary canal. The genital operculae are preserved and a trace of the proximal part of the genital appendage can be seen, paired basal structures evident, but no detail of the distal part of the appendage is preserved.

The preabdomen is less clearly preserved on the counterpart than on the part. The medial fracture cuts obliquely across the body so that the lateral margins of the sternites are not clearly preserved. The first segment of the postabdomen is almost completely preserved with only its right lateral margin missing. The left half of the second postabdominal segment and only an anterolateral corner of the third are preserved. The more posterior postabdominal segments and the telson are not preserved on the counterpart.

Specimen GSSA C427 (paratype). The part displays portions of the posterior three sternites of the preabdomen, the right half of the postabdomen, the telson and an almost complete sixth prosomal appendage

(Pl. 3, figs 2, 4; Text-fig. 4). Because of an oblique fracture, the anterior half of this specimen and the left lateral margins of the five segments of the postabdomen are missing. The pretelson has a faint impression preserved in the medial region, expanding towards the posterior into a depression, representing the anal opening. All of the telson is preserved except for the left lateral margin.

Appendage VI is well preserved on GSSA C427a, more completely than on the holotype, with the distal seven podomeres present (Pl. 3, fig. 4; Text-fig. 4). Appendage VI is an elongate and slender structure with a prominent spine on the distal margin of podomere 8. Only a small corner of podomere 2 is present. Podomeres 3 and 4 are fully preserved: podomere 3, length 5.3 mm, width 4.5 mm, is square, whereas podomere 4, length 6.0 mm, width 4.9 mm, is more rectangular. The posterior margins of podomere 5, length 7.9 mm, width 5.6 mm, and podomere 6 have broken away. Podomere 6, length 8.6 mm, width 6.0 mm, is relatively long, and widens distally to 6.8 mm. Podomere 7, length 7.1 mm, width 7.1 mm, is somewhat broader than the preceding podomeres. A small triangular podomere, length 3.3 mm, width 2.2 mm (7a), projects off its distal margin. Podomere 8, width 5.6 mm, is elongated into two distal projections, the anterior projection giving this podomere an anterior length of 10.9 mm, twice that of the length of the posterior projection, only 5.3 mm long. The distal margin of podomere 8 is deeply emarginated between these two projections and a long, slightly curved terminal spine, length 4.9 mm, width at base 1.5 mm, projects to the length of the anterior projection of podomere 8. Patches of the original light brown cuticle are preserved on the terminal spine and the seventh and eighth podomeres.

On the counterpart, GSSA C427b, (Pl. 3, figs 1, 3; Text-fig. 4), parts of the posterior three preabdominal sternites are evident. Only a small corner of sternite 4 is preserved. The lateral margins of the anterior two sternites are indistinct, although their lengths can be measured: sternite 5, length 10.1 mm; sternite 6, length 10.1 mm; sternite 7, length 5.2 mm, width 31.4 mm. The postabdomen is more completely preserved on the counterpart than on the part, although the left lateral margin is still indistinct. The dimensions of the postabdominal segments of this specimen are: segment 1, length 4.9 mm, width 26.2 mm; segment 2, length 5.6 mm, width 24.7 mm; segment 3, length 5.6 mm, width 23.2 mm; segment 4, length 5.2 mm, width 19.9 mm; segment 5 (pretelson), length 8.2 mm, width 16.1 mm. Arthrodial membrane, 1.5 mm long, can be discerned between the posterior two postabdominal segments. It is highly wrinkled in places, reflecting the easier deformation of this softer cuticle. A medial impression, 1.1 mm wide and slightly concave, is present on the last three postabdominal segments, opening into a depression towards the posterior of the pretelson, representing the gut and anal opening. The telson, length 33.3 mm, width at base 11.2 mm, is more completely preserved than on the part, although the tip is obscured by sediment. Medially, two ridges in the proximal half of the telson, giving an M-shaped cross section, converge approximately half way down its length into a single ridge which gradually thins towards the tip of the telson (Pl. 3, fig. 1). This ridge represents internal soft tissue infilling the mould of the medial carina. Appendage VI is less completely preserved on the counterpart. Only podomeres 4–8 are apparent, together with the distal spine.

Remarks. In comparison with related forms, *O. augusti* is of intermediate size, more closely resembling *O. pumulis* in the lack of epimeral prolongations of the pretelson. The proportions of the prosoma and preabdomen are comparable in *O. augusti* and *O. kokouoensis*, although these tagma are a little broader, in proportion to their length, in *O. pumulis*. The postabdomen and telson are a little shorter in *O. augusti* than in the other species. The shape of the telson differs considerably in each taxon: that of *O. augusti* is lanceolate; that of *O. kokouoensis* is clavate (slight broadening in posterior half); and that of *O. pumulis* is long and styliform.

The posterior prosomal appendage is characteristic of these eurypterids, although the distal podomeres are not known in *O. pumulis*. A distinctive feature of *O. augusti* is the morphology of the terminal podomere of appendage VI. The distal margin of this podomere is drawn into two large projections, the anterior much larger than the posterior. The shape of this podomere and the long terminal spine, proportionally much larger than that of *O. kokouoensis*, are distinctive features of this new taxon.

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